Experimental evidence for friction-enhancing integumentary modifications of chameleons and associated functional and evolutionary implications

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The striking morphological convergence of hair-like integumentary derivatives of lizards and arthropods (spiders and insects) demonstrates the importance of such features for enhancing purchase on the locomotor substrate. These pilose structures are responsible for the unique tractive abilities of these groups of animals, enabling them to move with seeming ease on overhanging and inverted surfaces, and to traverse inclined smooth substrates. Three groups of lizards are well known for bearing adhesion-promoting setae on their digits: geckos, anoles and skinks. Similar features are also found on the ventral subdigital and distal caudal skin of chameleons. These have only recently been described in any detail, and structurally and functionally are much less well understood than are the setae of geckos and anoles. The seta-like structures of chameleons are not branched (a characteristic of many geckos), nor do they terminate in spatulate tips (which is characteristic of geckos, anoles and skinks). They are densely packed and have attenuated blunt, globose tips or broad, blade-like shafts that are flattened for much of their length. Using a force transducer, we tested the hypothesis that these structures enhance friction and demonstrate that the pilose skin has a greater frictional coefficient than does the smooth skin of these animals. Our results are consistent with friction being generated as a result of side contact of the integumentary filaments. We discuss the evolutionary and functional implications of these seta-like structures in comparison with those typical of other lizard groups and with the properties of seta-mimicking synthetic structures.

1. Introduction

The adhesive pads of gekkotan (Gekkota) and anoline (Dactyloidae) lizards have been well studied [1–6]. The adhesive setae of gekkotans evolved convergently multiple times [7,8], and those of gekkotans and anoles interact reversibly with the locomotor substratum to promote attachment [7,9] under the control of specific patterns of governance [5,10]. The squamate adhesive system, particularly that of geckos, has attracted the attention of evolutionary and functional morphologists [1,7,8,11–16], and those interested in biomimetics [9,17–22].

Studies of geckos are now beginning to reveal how the entire adhesive complex may have arisen [8]. Indications are that early phases in the elaboration and modification of the subdigital integument may have been associated with the enhancement of frictional interaction between the feet and the locomotor substratum [23]. Such modifications appear to occur in anatomically localized regions at which interaction between the substratum and the integument is particularly intimate [23]. It has been postulated that the development
of regionally and zonally specialized outer epidermal spinules on the ventral surface of the feet and digits served as the precursors for the more highly elaborate setae, and that these may have had functional relationships with the substrate that were later exapted as adhesive modifications [13,23].

Because of the phenomenal adhesive capabilities that geckos (and anoles) exhibit, attention has been almost exclusively devoted to understanding the form and function of fully expressed, adhesion-inducing setae [1,15,24–28]. Van der Waals forces and specific forms of shear-based frictional interaction are responsible for setal adhesion [5,9,18,19,22,29]. The possible friction-enhancing role of the potential precursors, however, has received only theoretical attention [23]. It is noteworthy, in this regard, that synthetic microfibrillar materials have been developed that dramatically enhance friction, permitting strong attachment under zero normal load [30,31].

Our search for a vehicle to assist in understanding the functional transition from friction-enhancing epidermal outgrowths to adhesion-inducing setae led us to a group of lizards that would evidently benefit from enhanced frictional interaction with the locomotor substratum: chameleons. Independent acquisition of functional characteristics (analogues) in distantly related lineages can be powerfully instructive in the interpretation of functional transitions. Chameleons are known for their prowess in negotiating narrow, and often steeply inclined, perches [2,32,33] and for moving slowly but assuredly on trees and bushes [33–36]. To do this, they employ uniquely configured zygodactylous feet [37] and a prehensile tail [33,38]. Herrel et al. [33] examined grasping in chameleons and found that arboreal species have a more powerful grip than do terrestrial species, and have hands and feet with relatively greater surface area than their terrestrial counterparts. They suggested that habitat use drove the evolution of autopodial morphology through its effects on performance. Enhanced gripping strength was attributed to the mechanical configuration of the feet and tail [33], with increased surface area promoting increased contact and positively affecting frictional and adhesive forces.

Lange [39] reported the presence of ‘epithelial fibre hairs’ on the ventral digital surfaces of Chamaeleo vulgaris, and these observations were subsequently verified [40–42], and the form of the microornamentation on the digits and subcaudal scales described. Spinner et al. [42] noted that the form and configuration of both the digits and the seta-like derivatives [39–41] of chameleons are morphologically different from those of gekkotans and anoles, and suggested that they may function differently in locomotion. They proposed that the structure of the feet and the tail, their mode of mechanical interaction with branches (the typical support surfaces), and the nature of the seta-like outgrowths pointed towards a friction-enhancing rather than an adhesion-inducing interaction. The non-directional orientation of the seta-like structures of chameleons was posited to be favourably disposed to the enhancement of frictional interactions, with the perpendicular shafts and flexible tips of the epidermal outgrowths probably able to induce frictional interactions in all directions.

Based upon previous suggestions [39–42], we tested the hypothesis that the integument of the ventral surfaces of the manus and pedes, and that of the distal subcaudal area, of chameleons enhances frictional interactions with surfaces they contact. To do so, we examined the ventral manual, pedal and caudal integument of chameleons and compared these to the features of the integument of other regions of the body to both confirm earlier morphological findings [39–42] and obtain force measurements of the interaction between the integument and a test surface. We devised a means of testing the interactions between these surfaces using a probe designed to measure frictional interactions at a scale commensurate with the dimensions of the integumentary outgrowths.

2. Material and methods

(a) Gross morphology and histology

The gross morphology of the manus and pes of spirit-preserved specimens of Chamaeleo africanus was examined using a Zeiss stereo microscope (Zeiss Stemi DV4). Specimens of Ch. africanaus were captured and sacrificed for histological examination. Manus and pedes were fixed in 10% neutral buffered formalin or in Bouin’s fluid [43]. 10 × 5 mm patches of skin were excised, washed overnight in distilled water, dehydrated in an ethanol series from 70 to 100%, cleared in xylene, and infiltrated with (two or three changes) and embedded in, paraffin wax (melting point 56–58°C). Seven to nine micrometre thick histological sections were cut with a manual rotary microtome (Erma Type RA–303). Haematoxylin and eosin staining was employed [43]. The sloughing cycle of living individuals was recorded so that the shedding cycle of the skin could be documented and related to the histological data.

(b) Scanning electron microscopy

Skin samples from spirit-preserved specimens of Ch. africanus Chamaeleo calyptratus, Calumma parsonii, Furcifer verrucosus and Furcifer oustaleti were examined. Samples were removed from the following areas: dorsal and ventral skin of the manus and pedes in the area of the fused and free portions of the digits; dorsal, lateral and ventral skin of the tail at the proximal and distal ends of that appendage; dorsal and ventral regions of the antebrachium and crus. Samples were placed in histological tissue baskets and surface debris was removed by immersion in distilled water in a sonicating bath. Samples were then cellophane-striped using adhesive tape to remove remaining surface debris and loose epidermis. They were then fully dehydrated by immersion (for 30 min each) in 85% ethanol, 100% ethanol (twice), 25% hexamethyldisilazane (HMDS), 50% HMDS, 75% HMDS and 100% HMDS (twice). They were then placed on an absorbent surface (a Kimwipe) in a fume hood for 10 min to allow the remaining HMDS to evaporate, left to air dry overnight, and then affixed to aluminium scanning electron microscopy (SEM) stubs with carbon tape, and sputter coated with gold alloy (20 nm thick gold/palladium film, 82% Au/18% Pd) using a Polaron SC7640 Sputter Coater. Skin samples were examined using a Zeiss EVO60 SEM. Images were acquired at 2048 × 1536 pixel resolution and saved in TIFF format. Additional samples of Ch. calyptratus were dehydrated by immersion in 100% ethanol (2 × 30 min), placed in specimen capsules containing 100% ethanol and critical-point dried, mounted on aluminium stubs using copper double-sided tape and silver conductive paint, gold/palladium (20 nm thick film) coated using a Polaron SC515 SEM coating system, and viewed on a JEOL6400 SEM. Images were acquired using Olympus Scandium Universal SEM Imaging software.

(c) Friction force measurements

We measured friction forces on the ventral and dorsal sides of the hands and feet of two living specimens of Ch. calyptratus. To test small areas of skin from the ventral and dorsal surface of the hands and feet, we restrained the specimens as follows. We lined an open box with bubble wrap and placed each animal on the cushioning lying on its left side. Using broad (5 cm
Figure 1. Force measurement set-up. The experimental animals were restrained using broad rubber bands, with one limb exposed to the spherical force transducer probe. The force transducer was mounted onto a motorized stage controlled by a computer. The normal force was predefined using feedback loops, whereas the friction force was measured as the probe was moved in a proximal–distal or lateral–medial direction (see arrows in inset). Three areas (P, proximal; M, middle and D, distal) of the ventral and dorsal skin of the feet were probed. (Online version in colour.)

3. Results

(a) Gross morphology and histology (figure 2a,b)

The digits of chameleons are opposable (figure 2a) and are grouped into zygodactylous clusters, with I, II and III opposing IV and V in the manus, and I and II opposing IV and V in the pes. They are fused basally but separate distally and bear strong, curved claws. The ventral and dorsal surfaces of the manus and pes are clad in juxtaposing tubercular scales, separated by narrow hinge regions. Histological images reveal that the ventral tubercles carry straight-shafted, seta-like structures on the Oberhäutchen layer (figure 2b). The selected representative stage, stage six of the sloughing cycle, shows the replacement seta-like structures forming in the renewing layers of the epidermis. They follow the general pattern of integumentary renewal through the sloughing cycle \cite{44}; thus, the inner Oberhäutchen layer carries the derivatives of the replacement generation.

(b) Statistical analysis

We used customized routines and the statistical toolbox of MATLAB, v. 7 (Mathworks, USA) to analyse and statistically compare results. We tested the data for normal distribution using the Lilliefors test. When comparing two samples against each other, we used either the Student’s \(t\)-test or the Mann–Whitney \(U\)-test as parametric and non-parametric tests, respectively. Test results are either stated in the text or are indicated in the figures.
We investigated the ventral areas of the manus, pes and tail and, as controls, skin from the dorsum of these same areas. SEM imaging reveals that the ventral surface of the hands and feet (figure 2c–g) carry short seta-like structures that resemble setae found on subdigital scales of anoline lizards [2,23]. They form a continuous pile on the ventral scales. Their shafts taper gradually and the distal tips may be rounded and slightly globular or more attenuated. They attain maximum lengths of 13–14 μm in Ch. Africanus, 8–9 μm in Ca. parsonii, 14–16 μm in Ch. Calyptratus, 7.5–8.7 μm in F. verrucosus and 10–11 μm in F. oustaleti. For species examined by us and Spinner et al. [42], reported length dimensions of the longest epidermal outgrowths are very similar. The diameters of these seta-like structures range from 1.3 to 1.8 μm at the base and 0.7 to 1 μm at the tip. They are densely packed, with approximately 800 000–900 000 filaments mm⁻². Such structures cover all scales in the area encompassed by the fused digits and are also present on the distal, short, free parts of the digits. On the prehensile tail (figure 3a–d), the scales of the lateral and ventral surfaces bear similar pilose surfaces, with outgrowths of comparable length to those of the manus and pes of each particular species. Generally, on each tubercular scale, the seta-like structures are the longest at the most elevated part of the dome and gradually decrease in length and become more tapered distally as the hinge region is approached, ultimately grading into spines and spinules on the lowest points of relief of these scales (figure 3e). On the tail, the same pattern is evident on the ventral and lateral scales of the distal region. An identical pattern of distribution and form of these structures is evident in all of the species of chameleon examined. Other regions of the body exhibit scales that lack these elongated filamentous structures, and are essentially smooth or bear only minute spinules (figures 2d and 3f). The observations thus indicate that the epidermal filaments are restricted in their distribution and occur only on areas that routinely directly contact the locomotor substratum. These results accord with those presented by Müller & Hildenagen [41] and Spinner et al. [42].
After confirming the presence of seta-like structures on the ventral skin of the manus and pes and the distal portion of the tail, we measured the frictional forces generated by these structures on the ventral surface of the manus, and the frictional forces generated by the epidermis on the dorsal surface of the manus (figure 1). There were no significant differences between outcomes for the directions in which we probed the same location (proximal–distal versus mediolateral directions: Student’s *t*-test: *t* = −1.5, d.f. = 29, *p* = 0.14), nor between the different locations that we tested on the ventral manual scales (proximal versus medial, Student’s *t*-test: *t* = 1.03, d.f. = 8, *p* = 0.66; proximal versus distal: *t* = 2.5, d.f. = 9, *p* = 0.06; medial versus distal: *t* = 0.9, d.f. = 9, *p* = 0.76). Thus, we pooled the data for the ventral scales. Figure 3a shows the frictional forces exhibited by the ventral and dorsal surfaces (i.e. in the presence and the absence of the hairs) under varying load. For each load, the ventral surface showed higher frictional forces than the dorsal one (for 1 mN, *p* = 0.0127; 5 mN, *p* = 0.0030; 10 mN, *p* = 0.0024; 20 mN, *p* = 0.0030: Mann–Whitney *U*-tests), with a strong relationship of frictional force to the applied load. However, as we found that the signal-to-noise ratio of our force transducer did not allow for precise measurements under the smallest load (1 mN), we excluded those measurements from the pooled data. The average frictional coefficient (μ = *F*<sub>x</sub>/*F*<sub>v</sub>) for the pooled measurements of the ventral manual scales was significantly greater than that for the dorsal manual scales (μ = 0.21 ± 0.06 and μ = 0.10 ± 0.08, respectively; independent *t*-test: *t* = 3.52, d.f. = 25, *p* = 0.0016; figure 4b), indicating enhanced frictional capacity associated with the seta-like structures.

The ventral and dorsal manual and pedal skin bear scales with a similar tubercular form, although the dorsal scales lack the seta-like structures. To test whether the differences in frictional capacity of the ventral and dorsal manual skin relate to a potential difference in the relative softness of the skin in these locations, and to test the hypothesis that frictional attributes of the ventral manual integument are owing solely to the presence of the seta-like structures that it bears, we tested the same sample of scales (from the ventral side of the hand) before and after scraping away the outer epidermal layer, thus removing the seta-like structures. The frictional forces of the scales with intact outgrowths were greater than those generated once they had been removed. Whereas the highest normal load used (5 mN) yielded a significantly different (paired *t*-test: *t* = −3.5, d.f. = 7, *p* = 0.0096) frictional coefficient (μ = *F*<sub>x</sub>/F<sub>v</sub> = 0.22 ± 0.022 before scraping and 0.19 ± 0.038 after scraping; figure 4c), the lower normal loads (1 and 2 mN, respectively) showed only a trend towards...
greater forces for the scales prior to scraping. It is likely that the higher noise-to-signal ratio of our force measurements for the lower normal forces was responsible for the absence of significant differences at these levels.

4. Discussion

Our results clearly indicate that for all species of chameleon examined there are differences in the expression of the morphology of the outer epidermal generation and that these differences are regionally specific, a finding that accords with those of previous investigators [40–42]. Elongated seta-like structures characterize the scales of the plantar surfaces of the hands and feet, and the ventral and ventrolateral surfaces of the distal part of the tail. Other areas of the body lack these outgrowths. The skin regions bearing these filamentous derivatives exhibit enhanced frictional capacity.

(a) The benefit of a friction-enhancing integument to chameleons

Chameleons typically (although not exclusively) occupy arboreal habitats, and all of the species examined by us are arboreal. Exploitation of relatively narrow branches using erect limbs and a narrow trackway [2,32,36] is associated with gross morphological adaptations that permit this pattern of locomotion [2,45]. Chameleons typically grasp the narrow and inclined perches upon which they move with zygodactylous digits [45] and the tightly coiled tail tip [38]. Grasping the surface in this way, and in this posture, may persist for prolonged periods while stationary and also occurs when climbing. A tight grasp of the perch [33] and the deployment of strong claws assists this, but there is likely to be slippage between the feet/tail and the perch that could be mitigated by enhancing the frictional interaction between the two [45].
Our observations indicate that such an enhancement of frictional interaction is brought about by regional integumentary modifications, whereby the outer epidermal generation is produced into densely packed fields of elongated, filamentous seta-like structures. The presence of these derivatives on the plantar surface of the hands and feet, and also on the ventral and ventrolateral surfaces of the distal, prehensile part of the tail, strongly suggests that the role of these is directly related to friction enhancement. These structures are similar to the setae of gekkotans and anoline lizards, but differences indicate that they are friction-enhancing rather than adhesion-inducing. Thus, the predictions of Spinner et al. [42] are consistent with our experimental observations.

(b) Comparison with the setae of other lizards

The filamentous structures of the pedal and caudal scales of chameleons are slender and bear globular, blunted or attenuated blade-like distal tips. They differ from the adhesion-inducing setae of gekkotans, anolines and scincids [1,27,28,46] in that no clear triangular spatulate tips are present. The spatulate structures described by Spinner et al. [42] are quite different in form from those of gekkotans and anolines and actually represent flattened, blade-like shafts rather than expanded tips borne on narrowed regions of much more slender shafts. Among chameleons, there may be a phylogenetic distinction between genera that exhibit (Furcifer, Calumma) and lack (Chamaeleo) these flattened, blade-like epidermal outgrowths, although Trioceros is apparently polymorphic in this regard [42]. A more complete phylogenetic survey is required to explore this question further, but it is evident that the flattened, blade-like outgrowths are not common to all chameleons. The integumentary, seta-like outgrowths of chameleons are not branched, are not directionally arranged and are not carried on distinctive subdigital pads that are divided into scansors or lamellae.

Chameleon ‘hairs’ are borne on tubercular scales that invest the entire ventral surface of the manus and pes (and the ventral and ventrolateral surfaces of the distal part of the tail) [42]. As such, they appear similar to the fields of elongated, attenuated spines on the basal regions of the digits and adjacent plantar regions of the manus and pes of the Tokay gecko (Trioceros, [23], figs. 4 and 5). Such tubercular scales, segregated by hinge regions [44], provide the skin with greater local flexibility and do not exhibit any directionality in terms of the orientation of the filamentous shafts.

Applying Peterson’s [2] and Peterson & Williams’s [47] system of terminology for filamentous integumentary outgrowths of squamates, the outgrowths of chameleons are most similar to prongs and seta/prong intermediates (those with flattened, blade-like shafts). Müller & Hildenhagen [41] employed this terminology in their description of chameleon integumentary filaments. The flattened, blade-like structures reported for Furcifer, Trioceros and Calumma by Spinner et al. [42] appear to be structures unique to chameleons, and do not fulfill the criteria for recognition as setae as defined earlier [2,47] and as routinely applied to structures encountered in gekkotans and anolines.

Phylogenetic relationships of the major taxa of lizards [48–50] suggest that the pilose epidermis of chameleons is derived independently from that of gekkotans, anolines and scincids, and thus represents the second expression of this general morphology within the Iguania. Similar integumentary derivatives have arisen at least three times in insects [51–54] and three times in spiders [55]. This commonality of form points to an optimized configuration for the enhancement of surface contact and, ultimately, attachment [56]. The seta-like structures of chameleons seemingly represent the hypertrophy of the spines [42] located in the hinge regions between tubercles and on less extensively modified scales (figure 3c,f).

(c) Functional attributes of the seta-like fields of chameleons

Our investigation of the surface interactive properties of the seta-like structures of chameleons showed no evidence of generation of adhesive forces and exhibited only increased frictional interaction with the probe. The form of the filaments, with attenuated, blunt or globose distal tips that are arranged in a gradational pattern (from peripheral to central) on the tubercular scales, appears to represent a favourable configuration for frictional enhancement, as suggested by Spinner et al. [42]. This pattern of distribution on tubercular scales is reminiscent of that on tubercular palmar scales of Tokay geckos [23]. These structures lack directionality, which is more expected of friction-enhancing capabilities than adhesion-inducing ones.

Our measurements demonstrate that the seta-like structures of chameleons impart a significant increase in the frictional coefficient of the integument. Such structures might be expected to decrease the surface area of contact, consistent with the lotus effect [57]. This raises an interesting question relating to the mechanism that underlies friction enhancement. Because we carried out our experiments using a smooth sphere as a probe, we can discount interlocking via a ‘Velcro-like’ mechanism. Geckos adhere using branched, spatulate-tipped setae that act as an array of angled beams [9,58], each ending in tiny strips of adhesive tape [22]. We propose that the friction-enhancing chameleon filaments depict what might be expected of a convergent transitional stage in the evolution of gekkotan and anoline adhesive setae, although they are also an adaptive solution in their own right. This concept is supported by the friction-enhancing gecko-like materials that have been engineered [30,31], which are remarkably similar in form to chameleon ‘setae’. The contact mechanics of these engineered materials have been explored in detail, and it has been found that friction enhancement on smooth surfaces is owing to a load-dependent increase in the contact area of the side of each fibre. Under low loads, the fibres are nearly vertical in orientation, contact the substrate only with their tips and contact across the substrate is incomplete because of variation in the lengths of the fibres. As the normal and shear loads increase, the fibres bend and contact the substrate along their sides [59]. This contact region grows as load increases, creating a ‘smart’ material response: friction increases as load increases. The broad, blade-like ‘setae’ of some chameleons reported by Spinner et al. [42] would probably further enhance frictional interactions by way of their bending and contacting the substratum along their enlarged, flattened faces. We measured frictional forces only in Ch. calyptratus, a species also examined by Spinner et al. [42], who, like us, found it to lack the broadened, blade-like outgrowths.

Such contact mechanics depend strongly on a match between the external load and the stiffness of the fibre array. A rough estimate of the force $F_0$, required to change...
the configuration of an elastic beam from an upright contact to a side contact is given by the formula of Euler:

\[ F_b = \frac{\pi^2 EI}{(KL)^2} \]

where \( E \) is the elastic modulus of the material, \( L \) is the second moment of area, \( L \) is the length of the beam and \( K \) is a factor related to the constraints on the beam. For a fibre with uniform circular cross section or radius \( r \), \( L = \pi r^4/4 \). For a fibre with one end fixed and the other end free to move laterally, \( K \approx 2.0 \), assuming a \( \beta \)-keratin modulus of 2.0 GPa [5,29,60,61]. Further studies will be needed to determine the precise values in chameleons. Taking \( r = 1.0 \mu \text{m} \) and \( L = 15 \mu \text{m} \), we find \( F_b = 17 \mu \text{N} \).

For the taxa experimentally examined, there are approximately 370,000 fibres mm\(^{-2}\) on the gripping surface of the palm. A grip pressure of 6.37 N mm\(^{-2}\) would be required to collapse the array fully and engage the fibres in a maximally friction-enhancing configuration. In this configuration, the fibres are flattened against the underlying surface, and the contact area increases relative to that of both an uncollapsed configuration and, presumably, that of a stiff, inflexible scale. Macroscopic friction, as described by Amonton’s Laws, is typically taken to be unchanged by the apparent size of the contact between objects. At the microscale, however, this is not the case, and the strength of individual contacts is proportional to their interfacial area [62]. The dense arrangement of the fibres on the feet and ventral caudal region of chameleons may permit them access to this microscopic regime, in which area-enhancing mechanisms can provide additional friction force. At grip pressures lower than the 6.37 N mm\(^{-2}\) required for full collapse, a lower but significant level of friction enhancement will occur. It remains to be determined what pressure values are present during climbing. As well, rough substrates may create stress concentrations that increase friction enhancement.

5. Conclusion

Our observations and experimental results indicate that regionally restricted filamentous integumentary arrays of chameleons are located in areas where friction enhancement would be of value in counteracting slippage when negotiating narrow and inclined perches. Furthermore, we demonstrate that the filamentous arrays exhibit enhanced frictional properties when compared with regions of the integument lacking these arrays. Our calculations of the properties of these arrays, and our discovery that they are non-directional in their responses, are consistent with friction enhancement of grasping structures. These findings also indicate that the adhesive setae of gekkotan and anoline lizards may have been evolutionarily preceded by friction-enhancing filaments—such structures are present in the non-adhesive areas of the feet of both of these taxa. Friction-enhancing filaments, in such a scenario, would have become reconfigured and associated with more active control mechanisms as transition to adhesion-inducing properties occurred.

The experiments carried out at Glasgow University were conducted in accordance with UK Legislation on Animal Experimentation.

Acknowledgements. We thank Jon Barnes for valuable discussions on the experiments, Diana Samuel for revising the manuscript, Jonathan Puthoff for help with predictions for fibre collapse and Erica Lai, Margaret Mullin and Jörg Hardege for assistance with scanning electron microscopy. The comments of three anonymous referees helped us to improve the substance of this paper.

References


